# Home range, habitat selection, and foraging rhythm in Mauritanian spoonbills (Platalea leucorodia balsaci)

El-Hacen, El-Hacen Mohamed; Overdijk, Otto; Lok, Tamar; Olff, Han; Piersma, Theunis

*Published in:*
Waterbirds

*DOI:*
10.1675/063.036.0305

# Home Range, Habitat Selection, and Foraging Rhythm in Mauritanian Spoonbills (*Platalea leucorodia balsaci*): A Satellite Tracking Study

El-Hacen Mohamed El-Hacen[1,2,*], Otto Overdijk[3], Tamar Lok[1,4], Han Olff[5] and Theunis Piersma[1,4]

[1]Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

[2]Parc National du Banc d'Arguin, Avenue Gamal Abdel Nasser, B.P. 5355, Nouakchott, R.I. de Mauritanie

[3]Werkgroep Lepelaar, Knuppeldam 4, 9166 NZ Schiermonnikoog, The Netherlands

[4]Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

[5]Community and Conservation Ecology, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

[*]Corresponding author; E-mail: e.h.m.el.hacen@rug.nl

**Abstract.—**Mauritanian Spoonbills (*Platalea leucorodia balsaci*) only breed at Banc d'Arguin, Mauritania, West Africa. Their populations have declined; however, nothing is known about possible ecological factors involved, including their primary food and foraging habits. Home range sizes, habitat selection, and foraging rhythm in six adult Mauritanian Spoonbills were documented by attaching backpack harnesses with solar-powered satellite GPS-transmitters. Based on 18 bird-months of data (5,844 selected ground positions) collected between 2008 and 2010, these individuals never left the study area centered on the island of Tidra. The fixed kernel home range size was 23-101 km$^2$ ($\bar{x}$ = 62 km$^2$) and the core area 2-14 km$^2$ ($\bar{x}$ = 7 km$^2$). Home range sizes did not differ between breeding and non-breeding seasons. Mauritanian Spoonbills fed only in intertidal areas where they preferred the seagrass-covered (*Zostera noltii*) areas and they fed primarily during the ebbing tide. Furthermore, the GPS-positions away from the high tide roosts were strongly associated with creeks dissecting the seagrass beds. During the non-breeding season, foraging occurred throughout the 24-hr period, but during the breeding season they foraged exclusively by night. *Received 30 July 2012, accepted 2 January 2013.*

**Key words.—**habitat selection, home range, intertidal mudflats, Mauritanian Spoonbills, *Platalea leucorodia balsaci*, population decline, seagrass, Threshkiornithidae, tidal rhythm, *Zostera noltii*.

Waterbirds 36(3): 277-286, 2013

In 1974, the Eurasian Spoonbills (*Platalea leucorodia*) that breed in the Parc National du Banc d'Arguin (PNBA), Mauritania, West Africa, received recognition as a separate subspecies, the Mauritanian Spoonbill (*P. l. balsaci*). This recognition was based on morphological differences from the nominate subspecies breeding in Europe (*P. l. leucorodia*) (de Naurois and Roux 1974); recently, genetic data validated this subspecies assignment (Piersma *et al.* 2012). Unlike the European-breeding relatives (*P. l. leucorodia)* that show a wide range of migration strategies (Cramp and Simmons 1977; Lok *et al.* 2011), Mauritanian Spoonbills appear sedentary, rarely being reported outside Banc d'Arguin. The Mauritanian subspecies remains one of West Africa's lesser known waterbirds.

Mauritanian Spoonbills are currently declining (Veen *et al.* 2012). Breeding numbers decreased from 1,943 breeding pairs in 2000 (Overdijk *et al.* 2001) to 750 breeding pairs in 2007 (Triplet *et al.* 2008). The Mauritanian Spoonbill population exhibits low levels of recruitment that appear linked to the frequent occurrences of the colony-wide desertion of nests (Veen *et al.* 2012). However, other contributing factors such as problematic feeding conditions and spatial aspects of foraging ecology have not been assessed.

This study focuses on habitat use and foraging ecology of Mauritanian Spoonbills throughout the annual cycle. Until recently, most studies of habitat selection have involved marked individuals that have been followed on the ground or via VHF telemetry to compare what types of habitats animals are using in comparison with those available (Johnson 1980; Edge *et al.* 1987; Clark *et al.* 1993). Recent advances in satellite and GPS (Global Positioning System) tracking

technology, coupled with finer resolution satellite imagery, have greatly enhanced our ability to assess use of habitats (Dickson and Beier 2002; Jiguet and Villarubias 2004; Willems *et al.* 2009), especially in difficult to access regions. Data obtained through remote sensing have the added benefit of reducing disturbance to animals (at least after recovery from capture stress), which is likely important for Mauritanian Spoonbills given their propensity for nest desertion (Veen *et al.* 2012). Here we present results obtained from GPS transmitters used to track the annual-cycle movements of six adult Mauritanian Spoonbills over a 3-year period. We specifically report on total and seasonal home range size, habitat selection at a range of scales from general habitat types to microhabitats (creek courses), and daily foraging rhythms relative to roosting sites and diurnal tides.

## METHODS

### Study Area

The study was conducted in the Parc National du Banc d'Arguin, Mauritania (see Wolff *et al.* 1993; Campredon 2000). The area consists of about 491 km$^2$ of intertidal flats, including 93 km$^2$ covered by dense beds of seagrass (*Zostera noltii*) and 219 km$^2$ of mudflats partially or less densely covered by seagrass (based on 1984 data; Wolff and Smit 1990). The older seagrass-covered intertidal flats are characterized by the presence of circular pools (van der Laan and Wolff 2006) and small creeks. Larger channels separate the different mudflat areas.

### Satellite Tracking

During the breeding seasons of 2008 and 2009, we captured six adult Mauritanian Spoonbills on their nests using a "trap robe" and fitted them with solar-powered satellite GPS-transmitters (Model 30GPS, North Star Science and Technology) (Table 1). Birds were molecularly sexed using blood samples (T. Lok, unpubl. data). Each transmitter was attached to the individual's back using a harness made of Teflon ribbons (see Ueta *et al.* 2000). The transmitter was programmed to record and store data at 6-hr intervals, including data on position, position accuracy, speed, date, and time. Stored data were communicated via the ARGOS system (ARGOS 2011), which provides accuracy to < 100 m. However, the GPS transmitters could provide more accurate positions (± 15 m) (van der Winden *et al.* 2010; Chevallier *et al.* 2011). Locations were filtered in two steps based on the position accuracy and the speed. First, the most accurate locations were selected (< 26 m). Secondly, and to avoid flying birds in the analyses, only the slow fixes were included (speed < 4 m/s). A total of 5,844 GPS positions were then used for habitat selection and foraging rhythm analyses.

We partitioned GPS data into breeding and non-breeding phases of the annual cycle. We considered an individual to be breeding if it returned to its exact position more than two times per 24 hr on a known breeding site. These location data also allowed us to locate previously unknown or suspect breeding colonies (O. Overdijk, unpubl. data). To analyze movements of the birds, we used ArcGIS (Environmental Systems Research Institute 2009) in combination with Program R (R Development Core Team 2010).

### Home Range Estimation

We estimated individual home ranges using a robust non-parametric method, the fixed kernel estimator (KDE) (Worton 1989; Seaman *et al.* 1999), with the reference method ($h_{ref}$) for estimating smoothing parameter *h* (Seaman and Powell 1996). We defined the 95% kernel home range (95% KDE) as the global individual home range and the 50% kernel home range (50% KDE) as the core areas. To compare home range sizes during breeding and non-breeding seasons, we selected an equal number of random GPS locations for each season and then tested for differences using Wilcoxon's rank t-test.

### Habitat and Creek Selection

We developed our land-cover map from Landsat imagery (from 18 December 2001) based on the Normalized Difference Vegetation index (NDVI) (Tucker 1979; Barille *et al.* 2010). From this we classified four habitat types: 1) land (dunes); 2) seagrass beds; 3) sand-flats; and 4) sea, including the permanent channels (Fig. 1).

**Table 1. Details of the six adult Mauritanian Spoonbills (*Platalea leucorodia balsaci*) equipped with GPS transmitters in 2008 and 2009. Sex was determined from molecular assessment using Ellegren primers (Fridolfsson and Ellegren 1999). Observations ended on 12 February 2010.**

| Identification | Sex | Capture Site | Capture Date | No. of Fixes | Breeding Period (2009) |
|---|---|---|---|---|---|
| Hacen | male | Zira | 2 July 2008 | 5,980 | 15 Mar-10 July |
| Abou | male | Nair | 12 July 2008 | 5,822 | 13 Apr-7 Sept |
| Camara | male | Nair | 12 July 2008 | 6,621 | 21 Apr-23 Aug |
| Abdoul | female | Nair | 12 July 2008 | 5,593 | 13 May-16 July |
| Salem | unknown | Zira | 4 May 2009 | 3,313 | 5 May-21 Aug |
| Sidi | female | Zira | 4 May 2009 | 3,148 | 4 May-5 July |

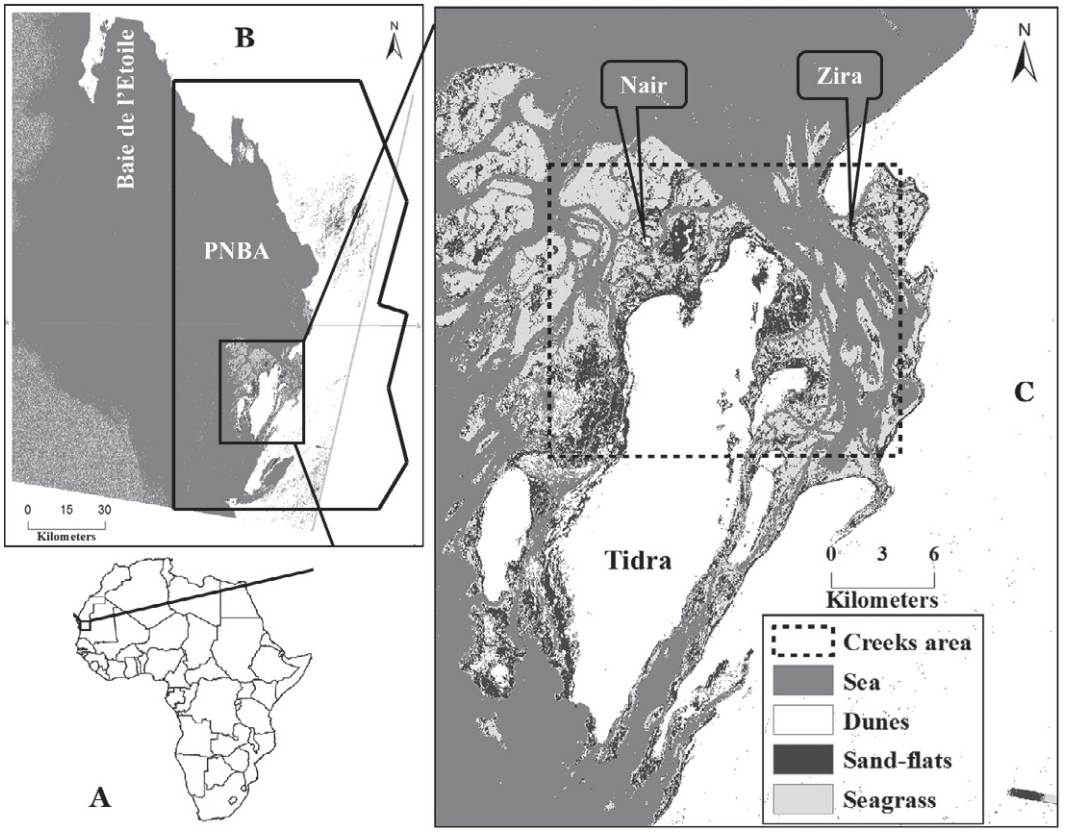


**Figure 1. Habitat types in the study area based on the Normalized Difference Vegetation index (NDVI) of the Landsat Image of 2001; the dashed square outlines the area analysed for creek effects (inset C).**

Dune habitat is known to be used only for roosting and was excluded from the analyses of feeding habitat selection. In order to investigate the preference of creeks as a feeding ground by Mauritanian Spoonbills, a Google Earth picture of approximately 20 by 20 km (creek zone) was selected based on its high quality and the intensive use by spoonbills. The creeks in this area were digitized in Google Earth, and then exported to ArcGIS for further analyses. In ArcGIS, we buffered the creek courses with a fixed width of 25 m using the Euclidean distance analysis tools. Then the GPS positions were overlaid onto the habitat types and the creek maps in ArcGIS (Minton *et al.* 2003; Galanti *et al.* 2006). The proportions of the different habitats and the numbers of GPS positions in each habitat/buffer were computed using the compositional analyses of the *Adehabitat* packages (Calenge 2006; R Development Core Team 2010). Pseudoreplication was not a concern since in compositional analysis the individual is the sample unit and not the telemetry locations (Aebischer *et al.* 1993).

To find evidence for habitat selection, we used the third order of compositional analysis (Aebischer *et al.* 1993) in which habitat selection is measured within the 95% KDE for each individual separately. For a possible preference to forage near and in creeks, we performed the second order (selection is measured at the population level) of compositional analyses (Aebischer *et al.* 1993), using 3,472 GPS positions that fell within the creek zone (Fig. 1).

### Foraging Rhythms

To determine if Mauritanian Spoonbills were roosting or foraging, we established a map of known or suspected high-water roost sites (after Overdijk *et al.* 2000) and used a birds' distance from the roost site as an indication of its activity. For example, a distance close to zero would indicate the bird was at the roost while increasing distance from the roost indicated the bird was likely en route to or at a foraging site. The distances to the nearest roosting site were tested for departure from normality using graphical inspection with QQ plots (Crawley 2007).

To assess foraging relative to the stage of the tide, we divided each 12-hr tidal cycle into hourly intervals and assigned GPS-location data to an hour class. We performed analyses of variance (ANOVA) to test the null hypothesis that all the distances to the nearest roost were equal for all the tidal time classes, and a Tukey HSD procedure was employed to report the statistical differences between the different tidal time classes. The local sunrise/sunset was shifting around 7:00 and 19:00 respectively. All foraging events that

took place between 7:00 and 19:00 were considered to be in the daytime foraging class; all other times were considered to be in the night-time foraging class.

## RESULTS

Home range sizes based on both 95% KDE and 50% KDE varied greatly among the six adults throughout their annual cycle, ranging from 23-101 km$^2$ ($\bar{x}$ = 62 km$^2$) and 2-14 km$^2$ ($\bar{x}$ = 7 km$^2$), respectively (Fig. 2). There was no significant difference in 95% KDE home range size between the breeding and non-breeding seasons (Wilcoxon ranked t-test, $P = 0.47$; breeding season $\bar{x}$ = 21.6 km$^2$, range 9-45.8 km$^2$; non-breeding season $\bar{x}$ = 31 km$^2$, range 6-55 km$^2$).

Habitat selection, calculated separately for each of the six birds (third order computation of 95% KDE), was not random (Wilks' $\lambda = 0.08$, $P = 0.002$), with birds preferring seagrass areas followed by sand-flats. Not surprisingly, sea (including permanent channels) was least preferred (Table 2). Within the preferred habitats, combining all individuals (second order computation of habitat selection), birds preferentially selected (Wilks' $\lambda = 0.03$, $P < 0.001$) areas within 25 m of creeks followed by areas 25-50 m from the creeks (Table 3).

For each bird separately, the distances to the nearest roosting site were plotted per hour class relative to low tide (Fig. 3). Most individuals showed a significant increase in the distance to the roosting site about 3 hr before the low tide (Table 4). One spoonbill

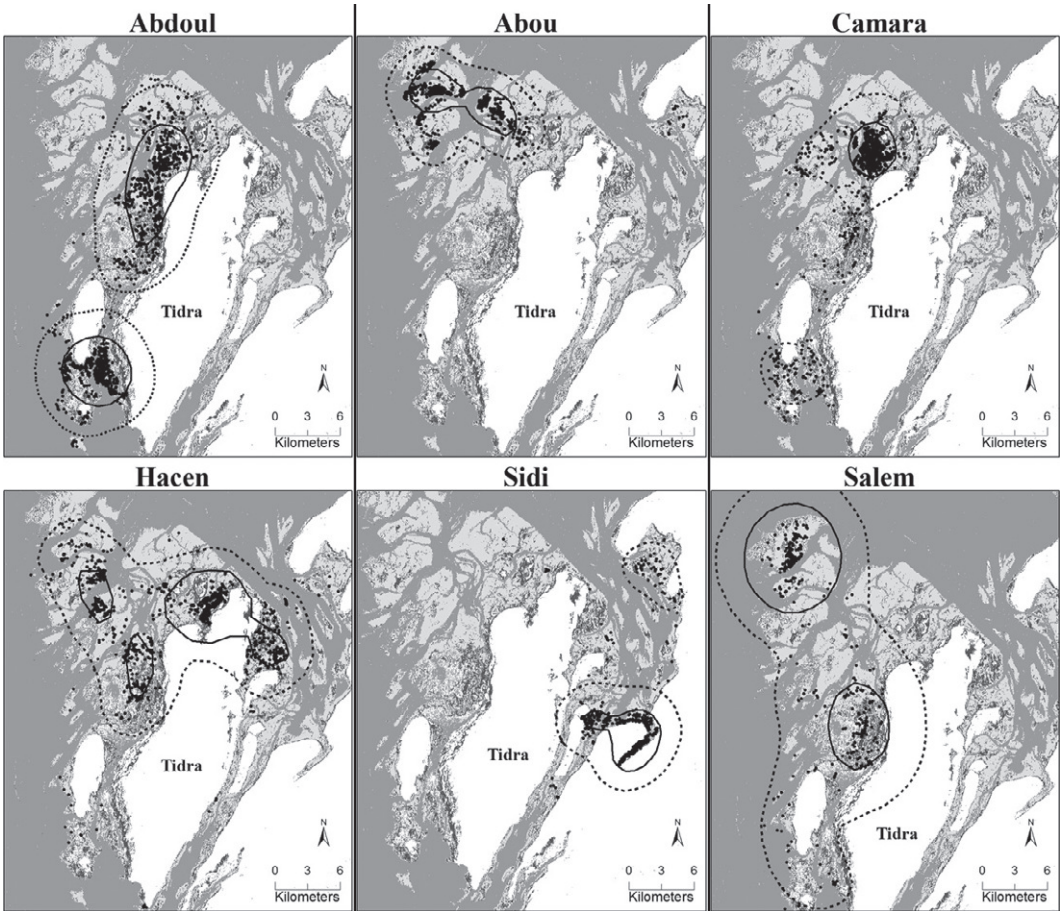


**Figure 2. The core 50% KDE (solid line) and 95% KDE (dashed line) for each of six Mautrianian Spoonbills (*Platalea leucorodia balsaci*) tracked during the study.**

**Table 2. Ranking matrices of habitat selection by GPS-tagged Mauritanian Spoonbills (*Platalea leucorodia balsaci*). Symbols at the intersection of a row and column indicate if the habitat in the row is preferred (+) or not preferred (-) over the habitat in the column. A significant difference is indicated by a triple sign.**

| Habitats | Seagrass | Sand-flats | Sea | Rank |
|---|---|---|---|---|
| Seagrass | 0 | +++ | +++ | 1 |
| Sand-flats | --- | 0 | +++ | 2 |
| Sea | --- | --- | 0 | 3 |

(identified as Sidi) showed a similar pattern, but in his case the increase was not statistically significant (Table 4); this spoonbill was feeding and roosting in a small area and used different sand banks as roosting places.

When breeding, the Mauritanian Spoonbills remained in their nests during the day (Fig. 4), while they foraged both diurnally and nocturnally during the non-breeding season (Table 4).

## DISCUSSION

Our satellite tracking over 3 years showed no movement of the six adult Mauritanian Spoonbills beyond the confines of PNBA. Nevertheless, we are aware of two instances of birds having ventured outside the Banc d'Arguin. In one case a juvenile, banded within PNBA in 2002, was observed 6 months later in the delta of the Senegal River (O. Overdijk, unpubl. data); in another case, an adult was reported in Baie de l'Etoile in northwestern Mauritania (Y. Diawara, unpubl. data). It is possible that the attached instruments and processes could have affected the individual birds' behaviors. However, multiple observations of these individuals nesting successfully (O. Overdijk and E. El-Hacen, unpubl. data) would argue against this.

We found the home ranges of these six birds to be restricted to relatively small parts of PNBA, with most birds using mainly the intertidal areas in the west and northwest portions of the island of Tidra (Fig. 2). Home ranges varied enormously between individuals, with two of the birds limiting their movements to small areas around their breeding sites, while the other four birds used a wider range of the available intertidal areas. Surprisingly, there was no difference in 95% KDE between the breeding and non-breeding seasons. Obviously, a sample size of six could not show the entire known feeding range of Mauritanian Spoonbills. For example, Mauritanian Spoonbills have been seen in places other than the intertidal areas around Tidra; including in Baie de Saint Jean in the south of PNBA as well as in the Baie d'Arguin in the north (E. El-Hacen *et al.* pers. obs.).

Our tracked Mauritanian Spoonbills selected seagrass beds over the other habitat types (Table 2). The selection probably reflects the distribution (Piersma 2012) and the mobility (Curio 1976) of their prey. Shrimps and prawns are known to be important prey for Mauritanian Spoonbills on Banc d'Arguin based on dropping analyses (Veen *et al.* 2012). These prey items are much more abundant on seagrass-covered substrates than on bare sandy intertidal substrates. Here, the three most abundant shrimp species were only captured in pools or in seagrass beds (Schaffmeister *et al.* 2006), and several fish and shrimp species occurred principally in seagrass areas (Maigret and Ly 1986; Jager 1993; Food and Agri-

**Table 3. Ranking matrices of the creek selection by GPS-tagged Mauritanian Spoonbills (*Platalea leucorodia balsaci*). Symbols at the intersection of a row and column indicate if the creek buffer in the row is preferred (+) or not preferred (-) over the creek buffer in the column. A significant difference is indicated by a triple sign.**

| Buffers | 25 m | 50 m | 75 m | 100 m | 125 m | > 125 m | Rank |
|---|---|---|---|---|---|---|---|
| 5 m | 0 | +++ | +++ | +++ | +++ | +++ | 1 |
| 50 m | --- | 0 | +++ | +++ | +++ | +++ | 2 |
| 75 m | --- | --- | 0 | + | + | +++ | 3 |
| 100 m | --- | --- | - | 0 | + | +++ | 4 |
| 125 m | --- | --- | - | - | 0 | +++ | 5 |
| > 125 m | --- | --- | --- | --- | --- | 0 | 6 |

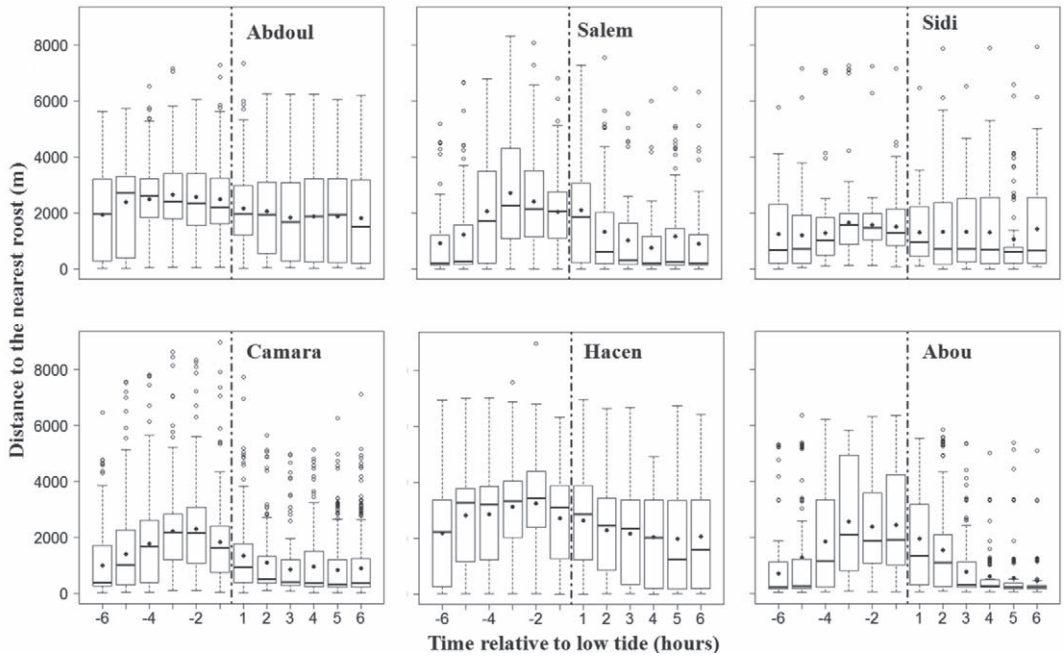


**Figure 3. Distance (m) of each of six tagged Mauritanian Spoonbills (*Platalea leucorodia balsaci*) to their nearest roost shown at hourly increments before (-) or after (+) low tide (dashed line). Dots in the boxes represent the mean.**

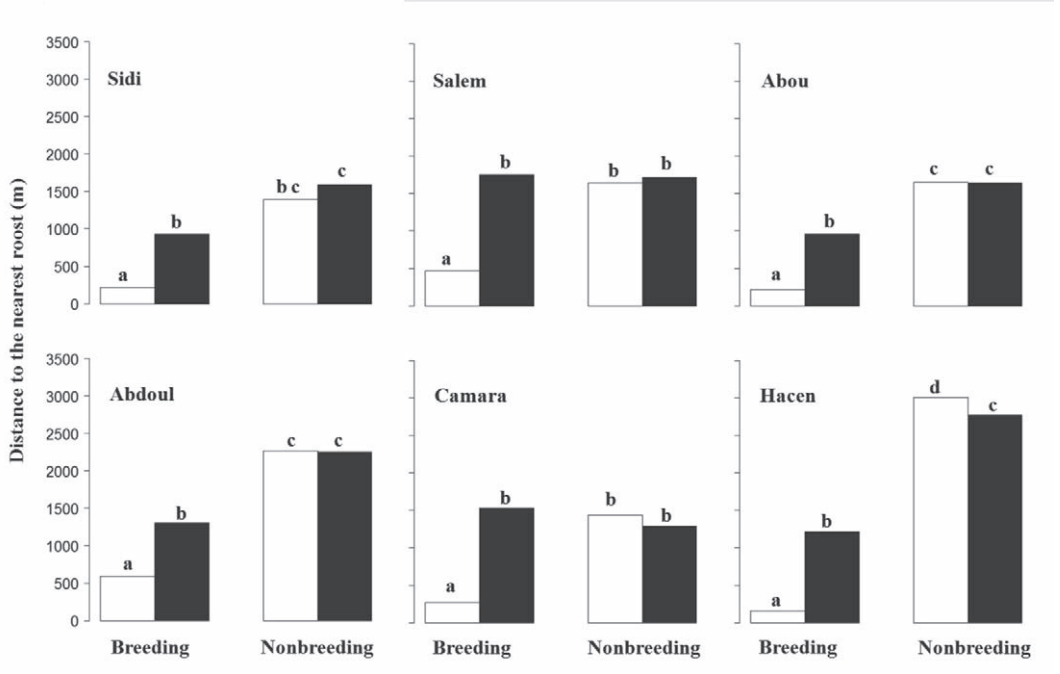


**Figure 4. A comparison in distance (m) to the nearest roost among tagged Mauritanian Spoonbills (*Platalea leucorodia balsaci*) during daytime (open) and nightime (filled) in both the breeding and non-breeding seasons. The letters above the bars denote a statistical comparisons; bars with different letters are significantly different.**

**Table 4. Results of ANOVA analyses on the foraging activities of the six tracked Mauritanian Spoonbills (*Platalea leucorodia balsaci*). "Distance" represents the distance to the nearest roost analysis, and "Day-night Foraging" represents activities during the non-breeding season.**

| | Distance | | | | Day–night foraging | | | |
|---|---|---|---|---|---|---|---|---|
| Identification | df | Residuals | *F* | *P* | df | Residuals | *F* | *P* |
| Hacen | 11 | 2,545 | 14.11 | < 0.001 | 1 | 2,553 | 63.6 | < 0.001 |
| Abou | 11 | 2,479 | 58.5 | < 0.001 | 1 | 2,487 | 22.1 | < 0.001 |
| Camara | 11 | 2,687 | 33.7 | < 0.001 | 1 | 3,695 | 58.9 | < 0.001 |
| Abdoul | 11 | 2,654 | 9.6 | < 0.001 | 1 | 2,662 | 9.4 | 0.002 |
| Salem | 11 | 1,023 | 14.3 | < 0.001 | 1 | 1,031 | 21.8 | < 0.001 |
| Sidi | 11 | 1,065 | 1.3 | 0.19 | 1 | 1,073 | 5.7 | 0.01 |

culture Organization of the United Nations 1998). During high tide, schools of fish and shrimp will move to the shallow tidal flats to feed, but during the ebb tide these animals will retreat toward the deep water and concentrate in the creeks. This may explain why, at a finer scale, Mauritanian Spoonbills selected the creeks for feeding (Table 3).

Mauritanian Spoonbills were not active during high tide (Fig. 3), even though on the highest flats the water depth would enable them to forage there. The tendency for waterbirds in tidal habitats to forage during the ebb tide has been shown before (Becker *et al.* 1993; Anderson *et al.* 2004; Thompson *et al.* 2005; Beauchamp 2009; Rey *et al.* 2010). Apart from the prey concentration effect discussed earlier, birds foraging with the ebb may benefit from tidal eddies. Such eddies will concentrate zooplankton and the fish species that feed on the zooplankton (Hamner and Hauri 1977; Alldredge and Hamner 1980; Gagnon and Lacroix 1983; Vermeer *et al.* 1987; Brown and Gaskin 1988; Wolanski and Hamner 1988).

As previously reported for spoonbill species around the world (Piersma 1980; del Hoyo *et al.* 1992; Yu and Swennen 2004), during the non-breeding season our marked birds foraged during both the day and night. Their foraging trips were shaped by tidal cycles rather than day-night cycles. However, during the breeding season the birds foraged almost exclusively at night and stayed around the nest site during the day (Fig. 4). McNeil *et al.* (1995) found that swimming prey are more abundant at night than during the day and concluded that tactile feeders would profit more by feeding at night. In Eurasian Spoonbills, males tend the eggs during the day and females at night, with the non-attending bird presumably going off to forage (Aguilera 1990). The Mauritanian Spoonbill individuals studied here fed almost exclusively at night during breeding, including the two females. The tendency for both sexes to remain at breeding colonies during the daytime may be driven by the need to guard against predatory gulls and terns that breed on the same islets (E. El-Hacen and O. Overdijk, pers. obs.). Dual-parent

attendance at breeding colonies may also be used to manage individual heat stress in hot environments, thus allowing one adult to periodically seek relief while the other tends the nest or chicks (Amat and Masero 2004; Tieleman *et al.* 2008; AlRashidi *et al.* 2010).

ACKNOWLEDGMENTS

We are very grateful to many people of the Parc National du Banc d'Arguin (PNBA) for hands-on help, and the international partners who provided the financial support for this study, especially la Fondation Internationale du Banc d'Arguin (FIBA), Vereniging Natuurmonumenten, the University of Groningen (an Eric Bleumink Fund grant to the first author), and Adessium Foundation. We thank R. Howison, W. Fokkema, A. Schlaich and C. Trierweiler for their help with the statistical and GIS analyses, P. de Goeij for comments and encouragement, and R.E Gill, Jr. and anonymous reviewers for editorial help. The procedures and research techniques on spoonbills at PNBA were evaluated and endorsed by the Conseil Scientifique du Parc National du Banc d'Arguin.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313-1325.

Aguilera, E. 1990. Sexual differences in nest attendance and chick-feeding rhythms of White Spoonbills. Auk 107: 416-420.

Alldredge, A. L. and W. M. Hamner. 1980. Recurring aggregation of zooplankton by a tidal current. Estuarine and Coastal Marine Science 10: 31-37.

AlRashidi, M., A. Kosztolanyi, C. Kupper, I. C. Cuthill, S. Javed and T. Szekely. 2010. The influence of a hot environment on parental cooperation of a ground-nesting shorebird, the Kentish Plover (*Charadrius alexandrinus).* Frontiers in Zoology 7: 1-10.

Amat, J. A. and J. A. Masero. 2004. How Kentish Plovers (*Charadrius alexandrinus*) cope with heat stress during incubation. Behavioral Ecology and Sociobiology 56: 26-33.

Anderson, C. D., D. D. Roby and K. Collis. 2004. Foraging patterns of male and female Double-crested Cormorants nesting in the Columbia River estuary. Canadian Journal of Zoology 82: 541-554.

ARGOS. 2011. ARGOS User's Manual. ARGOS Service, Toulouse, France. http://www.argos-system.org, accessed 19 August 2011.

Barille, L., M. Robin, N. Harin, A. Bargain and P. Launeau. 2010. Increase in seagrass distribution at Bourgneuf Bay (France) detected by spatial remote sensing. Aquatic Botany 92: 185-194.

Beauchamp, G. 2009. Functional response of staging Semipalmated Sandpipers feeding on burrowing amphipods. Oecologia 161: 651-655.

Becker, P. H., D. Frank and S. R. Sudmann. 1993. Temporal and spatial pattern of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. Oecologia 93: 389-393.

Brown, R. G. B. and D. E. Gaskin. 1988. The pelagic ecology of the Grey and Red-necked Phalaropes (*Phalaropus fulicarius* and *Phalaropes lobatus)* in the Bay of Fundy, eastern Canada. Ibis 130: 234-250.

Calenge, C. 2006. The package "*dehabitat*" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516-519.

Campredon, P. 2000. Entre le Sahara et l'Atlantique, le Parc National du Banc d'Arguin. FIBA, La Tour du Valat, Arles, France.

Chevallier, D., Y. le Maho, P. Brossault, F. Baillon and S. Massemin. 2011. The use of stopover sites by Black Storks (*Ciconia nigra*) migrating between West Europe and West Africa as revealed by satellite telemetry. Journal of Ornithology 152: 1-13.

Clark, J. D., J. E. Dunn and K. G. Smith. 1993. A multivariate model of female Black Bear habitat use for a geographic information system. Journal of Wildlife Management 57: 519-526.

Cramp, S. and K. E. L. Simmons (Eds.). 1977. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, vol. 1: Ostrich to Ducks, Oxford University Press, Oxford, U.K.

Crawley, M. 2007. The R book. John Wiley and Sons, London, U.K.

Curio, E. 1976. The ethology of predation. Springer Verlag, New York, New York.

de Naurois, R. and F. Roux. 1974. Précisions concernant la morphologie, les affinités et la position systématique de quelques oiseaux du Banc d'Arguin (Mauritanie). L'Oiseau et la Revue Française d'Ornithologie 44: 72-84.

del Hoyo, J., A. Elliott and J. Sargatal (Eds.). 1992. Handbook of the birds of the World. Lynx Edicions, Barcelona, Spain.

Dickson, B. G. and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. Journal of Wildlife Management 66: 1235-1245.

Edge, W. D., C. L. Marcum and S. L. Olson. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. Journal of Wildlife Management 51: 844-851.

Environmental Systems Research Institute (ESRI). 2009. ArcInfo and ArcMap v. 9.3. ESRI, Redlands, California. http:// www.esri.com/, accessed 25 April 2009.

Food and Agriculture Organization of the United Nations. 1998. Guide d'identification des ressources marines vivantes du Maroc. Food and Agriculture Organization of the United Nations, Rome, Italy.

Fridolfsson, A. K. and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30: 116-121.

Gagnon, M. and G. Lacroix. 1983. The transport and retention of zooplankton in relation to a sill in a tidal estuary. Journal of Plankton Research 5: 289-303.

Galanti, V. D., Preatoni, A. Martinoli, L. A. Wauters and G. Tosi. 2006. Space and habitat use of the African elephant in the Tarangire-Manyara ecosystem, Tanzania: implications for conservation. Mammalian Biology 71: 99-114.

Hamner, W. M. and I. R. Hauri. 1977. Fine-scale surface currents in the Whitsunday Islands, Queensland, Australia: effect of tide and topography. Australian Journal of Marine and Freshwater Research 28: 333-359.

Jager, Z. 1993. The distribution and abundance of young fish in the Banc d'Arguin, Mauritania. Hydrobiologia 258: 185-196.

Jiguet, F. and S. Villarubias. 2004. Satellite tracking of breeding Black Storks (*Ciconia nigra*): new incomes for spatial conservation issues. Biological Conservation 120: 153-160.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

Lok, T., O. Overdijk, J. M. Tinbergen and T. Piersma. 2011. The paradox of spoonbill migration: most birds travel to where survival rates are lowest. Animal Behaviour 82: 837-844.

Maigret, S. and B. Ly. 1986. Les poissons de mer de Mauritanie. Centre National de Recherches Océanographiques et des Pêches, Nouadhibou, Mauritania.

McNeil, R., O. D. Diaz, I. Linero and J. R. Rodriguez. 1995. Day-time and night-time prey availability for waterbirds in a tropical lagoon. Canadian Journal of Zoology-Revue Canadienne de Zoologie 73: 869-878.

Minton, J. S., J. N. Halls and H. Higuchi. 2003. Integration of satellite telemetry data and land cover imagery: a study of migratory cranes in Northeast Asia. Transactions in GIS 7: 505-528.

Overdijk, O., C. de la Court and A. Gueye. 2000. Spoonbill count on the Banc d'Arguin, Mauritania, January 2000. Working Group International Waterbird and Wetland Research (WIWO), Zeist, The Netherlands.

Overdijk, O., L. Marion and M. A. Sall. 2001. Spoonbill count on Banc d'Arguin, Mauritania, January-February 2001. Working Group International Waterbird and Wetland Research (WIWO), Zeist, The Netherlands.

Piersma, T. 1980. Lepelaars op de Mokkebank. Vanellus 33: 54-57.

Piersma, T. 2012. What is habitat quality? Dissecting a research portfolio on shorebirds. Pages 383-407 *in* Birds and Habitat: Relationships in Changing Landscapes (R. Fuller, Ed.). Cambridge University Press, Cambridge, U.K.

Piersma, T., M. van der Velde, E. M. El-Hacen, T. Lok and O. Overdijk. 2012. Molecular verification of the subspecies status of the Mauritanian Spoonbill (*Platalea leucorodia balsaci*). Ardea 100: 131-136.

R Development Core Team. 2010. R: a language and environment for statistical computing v.2.11.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org, accessed 31 May 2010.

Rey, A. R., C. A. Bost, A. Schiavini and K. Putz. 2010. Foraging movements of Magellanic Penguins (*Spheniscus magellanicus)* in the Beagle Channel, Argentina, related to tide and tidal currents. Journal of Ornithology 151: 933-943.

Schaffmeister, B. E., J. G. Hiddink and W. J. Wolff. 2006. Habitat use of shrimps in the intertidal and shallow subtidal seagrass beds of the tropical Banc d'Arguin, Mauritania. Journal of Sea Research 55: 230-243.

Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77: 2075-2085.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739-747.

Thompson, C. M., P. E. Nye, G. A. Schmidt and D. K. Garcelon. 2005. Foraging ecology of Bald Eagles in a freshwater tidal system. Journal of Wildlife Management 69: 609-617.

Tieleman, B. I., H. J. van Noordwijk and J. B. Williams. 2008. Nest site selection in a hot desert: trade-off between microclimate and predation risk? Condor 110: 116-124.

Triplet, P., O. Overdijk, M. Smart, S. Nagy, M. Schneider-Jacoby, E. S. Karauz, C. Pigniczki, S. Baha El Din, J. Kralj, A. Sandor and J. G. Navedo. 2008. International single species action plan for the conservation of the Eurasian Spoonbill (*Platalea leucorodia*). African-Eurasian Waterbird Agreement (AEWA), Bonn, Germany.

Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of Environment 8: 127-150.

Ueta, M., F. Sato, H. Nakagawa and N. Mita. 2000. Migration routes and differences of migration schedule between adult and young Steller's Sea Eagles (*Haliaeetus pelagicus*). Ibis 142: 35-39.

van der Laan, B. B. P. A. and W. J. Wolff. 2006. Circular pools in the seagrass beds of the Banc d'Arguin, Mauritania, and their possible origin. Aquatic Botany 84: 93-100.

van der Winden, J., M. J. M. Poot and P. W. van Horssen. 2010. Large birds can migrate fast: the post-breeding flight of the Purple Heron (*Ardea purpurea*) to the Sahel. Ardea 98: 395-402.

Veen, J., O. Overdijk and T. Veen. 2012. The diet of an endemic subspecies of the Eurasian Spoonbill *Platalea leucorodia balsaci*, breeding at the Banc d'Arguin, Mauritania. Ardea 100: 123-130.

Vermeer, K., I. Szabo and P. Greisman. 1987. The relationship between plankton-feeding Bonaparte's and Mew Gulls and tidal upwelling at Active Pass, British Columbia. Journal of Plankton Research 9: 483-501.

Willems, E. P., R. A. Barton and R. A. Hill. 2009. Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. Behavioral Ecology 20: 985-992.

Wolanski, E. and W. M. Hamner. 1988. Topographically controlled fronts in the ocean and their biological influence. Science 241: 177-181.

Wolff, W. J. and C. J. Smit. 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. Ardea 78: 17-38.

Wolff, W. J., J. van der Land, P. H. Nienhuis and P. de Wilde. 1993. The functioning of the ecosystem of the Banc d'Arguin, Mauritania–a review. Hydrobiologia 258: 211-222.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168.

Yu, Y. T. and C. Swennen. 2004. Feeding of wintering Black-faced Spoonbills in Hong Kong: when and how long? Waterbirds 27: 135-140.